

A finite-state continuous-time approach for inferring regional migration and mortality rates from conventional and archival tagging experiments

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SUMMARY

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Spatially-structured population dynamics models are important management tools for harvested, highly mobile species and while conventional mark-recovery experiments remain useful for estimation of various demographic parameters of these models, archival tagging experiments are becoming an important data source for analyzing migratory behavior of mobile marine species. We provide a likelihood-based approach for estimating the regional migration and mortality rate parameters intrinsic to these models that may use information obtained from conventional mark-recovery and archival tagging experiments. Specifically, we assume that the regional location and survival of animals through time is a finite-state continuous-time stochastic process. The stochastic process is the basis of probability models for observations provided by the different types of tags. Results from application to simu-

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12 lated tagging experiments for western Atlantic bluefin tuna show that maximum likelihood
13 estimators based on archival tagging observations and corresponding confidence intervals
14 perform similarly to conventional tagging observations for a given number of tag releases
15 and releasing tags in each region can improve the behavior of maximum likelihood estima-
16 tors regardless of tag type. We provide an example application with Atlantic bluefin tuna
17 released with conventional tags in 1990-1994.

18 **KEY WORDS:** finite-state continuous-time process; implanted archival tags; Markov process;
19 pop-up archival tags; spatially-structured population; tag-recovery

1. Introduction

Tagging experiments have proven to be powerful tools to gain demographic information from animal populations (Pollock, 1991; Schwarz and Seber, 1999; Seber and Schwarz, 2002). Statistical models are available to estimate a variety of parameters including abundance (Darroch, 1958), mortality (Hearn, Sundland and Hampton, 1987), size-specific harvest (Taylor, Walters and Martell, 2005) and growth rates (Laslett, Eveson and Polacheck, 2002). For populations of migratory animals that may be subjected to different levels of mortality in various regions, migration rates among adjacent regions have also been estimated through tagging experiments (e.g., Hilborn, 1990; Hestbeck, Nichols and Malecki, 1991; Schwarz, Schweigert and Arnason, 1993).

The statistical models for mark-recovery experiments usually consider release groups and recaptures made in discrete time where simplifying assumptions such as migration occurring only once and instantly between intervals and all tagged animals of a particular release group are released at the same time. Furthermore, many population dynamics models used to manage fisheries are parameterized with instantaneous mortality rates (e.g., Quinn and Deriso, 1999) and it would appear natural to consider migration in the same continuous time framework.

Mark-recovery experiments continue to be used widely to infer rates of movement and mortality of fish populations, but the relatively new popup satellite and implanted archival tags provide extensive observations of movements of pelagic migratory species (e.g., Block, Dewar, Blackwell, Williams, Prince, Farwell, Boustany, Teo, Seitz and Walli, 2001; Bonfil, Meÿer, Scholl, Johnson, O'Brien, Oosthuizen, Swanson, Kotze and Paterson, 2005) and allow inference of location continuously in time (e.g., Sibert, Musyl and Brill, 2003; Sibert, Lutcavage, Nielsen, Brill and Wilson, 2006). Because many species that are the subject of archival tagging studies may have been or continue to be the subject of conventional mark-recovery studies as well, a common estimation framework that can combine the information provided by these studies would be useful for their management.

47 To relax some unrealistic assumptions of models currently used to estimate migration
 48 rates from conventional mark-recovery experiments and also meet the need to allow in-
 49 formation from conventional and archival tagging studies to be combined, we provide
 50 likelihoods appropriate for conventional and archival tagging data to estimate instantaneous
 51 migration and mortality rates. To assess the behavior of maximum likelihood estimators
 52 (MLEs), we provide simulation results for experiments using different types of tags in a
 53 population of animals that migrates between two regions and experiences different levels of
 54 natural and harvest mortality in either region. We also, provide an example application to
 55 Atlantic bluefin tuna (*Thunnus thynnus*) conventional tagging studies.

56 2. Methods

57 2.1 *Finite-state continuous-time Markov processes*

58 Stochastic processes that describe the transition among a finite number of states in
 59 continuous time are referred to by various names including multi-state processes or finite-
 60 state continuous-time (FSCT) processes (Karlin and Taylor, 1975; Taylor and Karlin, 1984;
 61 Andersen et al., 1993). We use FSCT to emphasize the continuous-time aspect of these
 62 models and distinguish them from the discrete-time multi-state processes more commonly
 63 used to model mark-recapture experiments (e.g., Nichols and Kendall, 1995; Lebreton and
 64 Pradel, 2002). The fundamental characteristics of FSCT processes are the instantaneous
 65 intensities of transition between states $a_{h,i}(t) = \lim_{\delta t \rightarrow 0} P_{h,i}(t, t + \delta t) / \delta t$ where $0 \leq a_{h,i}(t) <$
 66 ∞ and $P_{h,i}(s, t) = P(Y(t) = i | Y(s) = h)$ is the probability that the process is in state
 67 $Y(\cdot) = i$ at time $t \geq s$ given it is in state $Y(\cdot) = h$ at time s (Andersen and Keiding,
 68 2002). In general, these transition intensities may change through time (non-homogeneous)
 69 and depend on the previous transition history of the process. We consider here the FSCT
 70 Markov process which is a class of FSCT processes where the instantaneous transition rates
 71 $a_{h,i}(s)$ depend only on the state at time s (Markovian) and are constant through time
 72 (homogeneous) or piece-wise constant through time.

73 The $H \times H$ infinitesimal matrix of *homogeneous* transition intensities, $\mathbf{A} = \{a_{h,i}\}$ has
 74 diagonal elements, $a_{h,h} = -\sum_{i=1, i \neq h}^H a_{h,i}$ and $-a_{h,h}$ are often termed hazards or forces of
 75 transition out of the corresponding states (Hoem, 1971). These requirements imply that
 76 each row of \mathbf{A} sums to zero. For homogeneous FSCT Markov processes, the probability
 77 transition matrix $\mathbf{P}(s, t) = \{p_{h,i}(s, t)\}$ is the exponential of the infinitesimal matrix

$$\mathbf{P}(s, t) = \exp\{\mathbf{A}(t - s)\} = \sum_{k=0}^{\infty} \frac{\{\mathbf{A}(t - s)\}^k}{k!} \quad (1)$$

78 where $t \geq s$ (e.g., Cox and Miller, 1965, pp. 178-186). The infinitesimal matrix can be
 79 diagonalized with its eigenvalues and eigenvectors so that the probability transition matrix
 80 can be calculated as $\mathbf{P}(s, t) = \mathbf{V} \exp\{\mathbf{D}(t - s)\} \mathbf{V}^{-1}$ where \mathbf{D} is a diagonal matrix of the
 81 eigenvalues and \mathbf{V} is the matrix of eigenvectors (Kalbfleisch and Lawless, 1985; Commenges,
 82 2002).

83 2.2 Defining states for animal populations

84 In general, an animal may at any instant, survive or die from one of several causes, but
 85 these outcomes may be further detailed. For example, in many studies we discretize the
 86 space where a migratory animal may be found so that the resulting regions correspond to
 87 habitats that the animals use for different purposes (e.g., breeding and feeding grounds) or
 88 areas used to manage harvest of the species (e.g., area-specific harvest limits). Within a
 89 discrete-space system, an animal may, at any instant, remain alive in a region, die from one
 90 of several causes in that region or move to any of the adjacent regions. If $\mathcal{H} = \{1, \dots, H\}$ is
 91 the set of states that an animal may exhibit, let \mathcal{R} , \mathcal{F} and \mathcal{M} represent the subsets of states
 92 where the animal is alive and in one of R regions, dead due to harvest in one of the R regions
 93 and dead due to other causes (i.e., natural mortality) in one of the R regions, respectively.
 94 We will use these subsets of states in formulating observation models for the three different
 95 types of tagging experiments below.

96 The FSCT framework we consider is a generalization of simpler FSCT Markov processes

97 assumed for many animal populations. For example, it is common in many population
 98 dynamics models for fish populations where migration is not considered, to assume animals
 99 either survive or die from natural or harvest mortality sources during a time interval τ . This
 100 equates to a process under our framework where there is a single region and two sources of
 101 mortality in that region. Letting F and M represent the instantaneous rates of transition
 102 (within τ) into the harvest and natural mortality states, respectively, the infinitesimal matrix
 103 for this process in the defined time interval is

$$\mathbf{A}(\tau) = \begin{pmatrix} -(F+M) & F & M \\ \mathbf{0} & \mathbf{0} & \mathbf{0} \end{pmatrix}$$

104 where $\mathbf{0}$ is a 2×1 column vector. The probability transition matrix for the interval that
 105 provides the probabilities of being in the living and two different mortality states at the end
 106 of the interval is

$$\mathbf{P} = \exp(\mathbf{A}\tau) = \begin{pmatrix} e^{-(F+M)\tau} & \frac{F}{F+M}\{1 - e^{-(F+M)\tau}\} & \frac{M}{F+M}\{1 - e^{-(F+M)\tau}\} \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix}. \quad (2)$$

107 When N_0 animals are alive at the start of the interval, the expected numbers in each state
 108 (product of N_0 and the probabilities in the first row of eq. 2) provides results widely known
 109 as the Baranov catch equations (Chapman, 1961; Ricker, 1975; Seber, 1982, p. 329). In fact,
 110 eq. 2 is the stochastic analog of the Baranov equations and these probabilities are general
 111 results for competing risks models with exponentially distributed life spans (Dupont, 1983;
 112 Kalbfleisch and Prentice, 2002, pp. 247-248). Similarly, for a population occupying two
 113 regions with migration rates μ_{12} and μ_{21} from regions 1 to 2 and 2 to 1, respectively, and no

114 mortality during the interval τ , the infinitesimal matrix,

$$\mathbf{A}(\tau) = \begin{pmatrix} -\mu_{12} & \mu_{12} \\ \mu_{21} & -\mu_{21} \end{pmatrix}$$

yields the probability transition matrix,

$$\mathbf{P} = \exp(\mathbf{A}\tau) = \begin{pmatrix} \frac{\mu_{21} + \mu_{12}e^{-(\mu_{12} + \mu_{21})\tau}}{\mu_{12} + \mu_{21}} & \frac{\mu_{12}}{\mu_{12} + \mu_{21}} \{1 - e^{-(\mu_{12} + \mu_{21})\tau}\} \\ \frac{\mu_{21}}{\mu_{12} + \mu_{21}} \{1 - e^{-(\mu_{12} + \mu_{21})\tau}\} & \frac{\mu_{12} + \mu_{21}e^{-(\mu_{12} + \mu_{21})\tau}}{\mu_{12} + \mu_{21}} \end{pmatrix},$$

115 where the diagonal provides the probabilities of an animal remaining in each region through
 116 the interval as demonstrated differently by (Whitehead, 2001, eq. 5) for a model to estimate
 117 abundance and migration rates for sperm whales.

118 2.3 Probability models for tagging experiments

119 The probability models we present below for observations derived from conventional tags,
 120 popup satellite archival tags (PSATs) and implanted archival tags (IATs) account for the data
 121 provided by the corresponding observations as functions of the instantaneous migration and
 122 mortality parameters. These probability models can also be combined to make likelihood-
 123 based estimates of the instantaneous parameters for studies that use multiple types of tags.

124 *2.3.1 Pop-up satellite archival tags* When PSATs are deployed on animals, they collect
 125 measurements of various environmental characteristics including light intensity until the tag
 126 releases from the animal and floats to the surface (pops up) where it relays information
 127 via satellite to the researcher. The tagged animal may theoretically be harvested prior to
 128 the pop-up time or the tag may pop-up when a tagged animal stays at a constant depth
 129 for specified amount of time because the animal is assumed dead (i.e., natural mortality).
 130 The relayed measurements of environmental characteristics can in turn be used to estimate
 131 geographic location of the tagged animal at a given time during the interval that the PSAT

132 was attached to the animal (e.g., Sibert et al., 2003).

133 When the ocean is compartmentalized into regions, the locations at time translate into
 134 regional occupation at time and times of migration between regions. Although the loca-
 135 tions are estimated rather than known, it may be safe to ignore the resulting uncertainty
 136 in times of migration between regions when the regions are large relative to the uncer-
 137 tainty in the locations and there should be no error in the times of harvest or natural
 138 mortality. Here we consider the migration times as known so that the data on a tagged
 139 animal k observed from the time the animal is tagged $t_{0,k}$ to the pop-up time $t_{a,k}$ are
 140 the times of transition, $\mathbf{t}_{I,k} = t_{1,k}, \dots, t_{l,k}, \dots, t_{n_k,k} : t_{0,k} \leq t_{l,k} \leq t_{a,k}$, and the states,
 141 $\mathbf{Y}_{I,k} = Y(t_{1,k}), \dots, Y(t_{l,k}), \dots, Y(t_{n_k,k}) : Y(t_{l,k}) \in \mathcal{H}$, the animal takes on during the period
 142 the tag is operating, $\tau_k = t_{a,k} - t_{0,k}$. Note that the set of states also includes natural and
 143 harvest mortality because the times of transition into these states may be observed for an
 144 animal with a PSAT. As these are data for a continuous-time observation of a FSCT process
 145 (Andersen et al., 1993; Andersen and Keiding, 2002; Commenges, 2002), the probability
 146 function for the set of observations from a PSAT is

$$\begin{aligned} \mathcal{P}_{I,k}(\mathbf{Y}_{I,k}, \mathbf{t}_{I,k} | t_{0,k}, Y(t_{0,k})) &= \prod_{l=0}^{n_k-1} \exp \left\{ \int_{t_{l,k}}^{t_{l+1,k}} a_{Y(t_{l,k}), Y(t_{l,k})}(t) dt \right\} a_{Y(t_{l,k}), Y(t_{l+1,k})}(t_{l+1,k}) \\ &\times \exp \left\{ \int_{t_{n_k,k}}^{t_{a,k}} a_{Y(t_{n_k,k}), Y(t_{n_k,k})}(t) dt \right\}. \end{aligned} \quad (3)$$

147 Notice in eq. 3 that the first line represent the product of probabilities of remaining in states
 148 between transition events and the transition to the next state. The second line of eq. 3
 149 represents the probability of remaining in the final observed state after the final observed
 150 transition. We assume that the release time ($t_{a,k}$) is fixed or at least independent of the
 151 process $Y(\cdot)$ in eq. 3 (i.e., an independent censoring time, cf. Andersen et al., 1993, Ch.
 152 III).

153 When the transition intensities are constant within the interval τ_k , eq. 3 reduces to

$$\mathcal{P}_{\text{I},k}(\mathbf{Y}_{\text{I},k}, \mathbf{t}_{\text{I},k} | t_{0,k}, Y(t_{0,k})) = \prod_{h=1}^H e^{a_{h,h}\tau_{h,k}} \prod_{i \neq h} a_{h,i}^{n_{h,i,k}} \quad (4)$$

154 where $n_{h,i,k} = \sum_{l=0}^{n_k-1} I(Y(t_{l,k}) = h, Y(t_{l+1,k}) = i)$ is the number of transitions from state
 155 h to state i and $\tau_{h,k} = \{\sum_{l=0}^{n_k-1} I(Y(t_{l,k}) = h)(t_{l,k} - t_{l+1,k})\} + I(Y(t_{n_k,k}) = h)(t_{a,k} - t_{n_k,k})$
 156 is the total amount of time spent in state h . Determining the MLE for the transition
 157 rate $a_{h,i}$ is straightforward (Albert, 1962) and asymptotic variance estimators have also
 158 been derived (Andersen and Keiding, 2002). When a piecewise-homogeneous model is used
 159 where transition rates are constant between time points $T_1, \dots, T_j, \dots, T_N$, some or all of
 160 the instantaneous rates may be interval-specific.

161 *2.3.2 Conventional tags* In conventional tag-recovery experiments, an animal is released
 162 with a unique tag and people harvesting the species may recover the tagged animal during the
 163 course of their efforts. Thus, given the state at time of release ($t_{0,k}$), we observe the time of
 164 recovery ($t_{r,k}$) and states immediately prior to ($Y(t_{r,k}-) \in \mathcal{R}$) and at recovery ($Y(t_{r,k}) \in \mathcal{F}$)
 165 for harvested animals. For unharvested animals, we know that the animal is either still
 166 alive or dead from natural sources at the time of analysis ($Y(t_{a,k}) \in \{\mathcal{R}, \mathcal{M}\}$). Note that
 167 $Y(t_{r,k}) = Y(t_{a,k})$ for recovered animals. Thus, the data are

$$\{\mathbf{Y}_{\text{II},k}, \mathbf{t}_{\text{II},k}\} = \begin{cases} \{Y(t_{r,k}-), Y(t_{r,k}), t_{r,k}\} & \text{if } Y(t_{a,k}) \in \mathcal{F} \\ \{Y(t_{a,k}) \in \{\mathcal{R}, \mathcal{M}\}\} & \text{otherwise} \end{cases}.$$

The probability function for the set of observations from a conventional tag is

$$\begin{aligned} \mathcal{P}_{\text{II},k}(\mathbf{Y}_{\text{II},k}, \mathbf{t}_{\text{II},k} | t_{0,k}, t_{a,k}, Y(t_{0,k})) &= \{P_{Y(t_{0,k}), Y(t_{r,k}-)} a_{Y(t_{r,k}-), Y(t_{r,k})}\}^{I(Y(t_{a,k}) \in \mathcal{F})} \\ &\times \left\{ \sum_{Y(t_{a,k}) \in \{\mathcal{R}, \mathcal{M}\}}^H P_{Y(t_{0,k}), Y(t_{a,k})} \right\}^{I(Y(t_{a,k}) \in \{\mathcal{R}, \mathcal{M}\})} \end{aligned} \quad (5)$$

168 where $I(Y(t_{a,k}) \in \mathcal{F})$ and $I(Y(t_{a,k}) \in \{\mathcal{R}, \mathcal{M}\})$ are indicators of whether the animal is in
 169 harvested and non-harvested states, respectively, at time of analysis. The first line in eq. 5
 170 is the product of the probability of being alive in region of recovery just prior to harvest at
 171 time $t_{r,k}-$ given $Y(t_{0,k})$ and the instantaneous rate of harvest in the region where recovery
 172 occurred. The probability $P_{Y(t_{0,k}), Y(t_{r,k}-)}$ is the $(Y(t_{0,k}), Y(t_{r,k}-))$ element of the probability
 173 transition matrix, $\mathbf{P}(t_{0,k}, t_{r,k}-)$ and $a_{Y(t_{r,k}-), Y(t_{a,k})}$ is the $(Y(t_{r,k}-), Y(t_{a,k}))$ element of the
 174 infinitesimal matrix. The second line in eq. 5 is the probability of being in any of the
 175 nonharvested states at the time of analysis given $Y(t_{0,k})$ which is the sum of the elements of
 176 the probability transition matrix $\mathbf{P}(t_{0,k}, t_{a,k})$ in row $Y(t_{0,k})$ where $Y(t_{a,k}) \in \{\mathcal{R}, \mathcal{M}\}$.

177 All tags are assumed to be reported here, but incomplete tag reporting could be incor-
 178 porated into the model by expanding and redefining the possible states. In application, we
 179 determine the maximum likelihood estimates using numerical methods similar to Kalbfleisch
 180 and Lawless (1985) where we determine the instantaneous rates and the probability transi-
 181 tion matrices using eq. 1 such that the required elements maximize eq. 5.

When a model is used where transition rates are piecewise-constant between time points
 $T_1, \dots, T_j, \dots, T_N$ and $j_{0,k} = \min\{j : T_j > t_{0,k}\}$ and $j_{r,k} = \max\{j : T_j < t_{r,k}\}$, the probability
 transition matrices required are the product of the interval-specific matrices,

$$\mathbf{P}(t_{0,k}, t_{r,k}) = \mathbf{P}(t_{0,k}, T_{j_{0,k}}) \mathbf{P}(T_{j_{0,k}}, T_{j_{0,k}+1}) \cdots \mathbf{P}(T_{j_{r,k}-1}, T_{j_{r,k}}) \mathbf{P}(T_{j_{r,k}}, t_{r,k}),$$

182 due to the Markov assumption. The probabilities necessary for an unrecovered tag are
 183 obtained by the product of the interval-specific matrices where $t_{a,k}$ is used instead of $t_{r,k}$.

184 *2.3.3 Implanted archival tags* Like conventional tags, IATs will remain in tagged ani-
 185 mals for the remainder of their lives and we only obtain post-release information from animals
 186 that are harvested. However, like PSATS, we can observe times of transition and states before
 187 the time of tag battery expiration ($t_{e,k}$) for a recovered animal ($\mathbf{t}_{1,k} = t_{1,k}, \dots, t_{l,k}, \dots, t_{n_k,k} :$

188 $t_{0,k} \leq t_{l,k} \leq t_{e,k}$, $\mathbf{Y}_{I,k} = Y(t_{1,k}), \dots, Y(t_{l,k}), \dots, Y(t_{n_k,k})$. If the animal is recovered after
 189 the battery expires, we also have an observation analogous to that of a conventional tag
 190 where the state at the time of battery expiration ($t_{e,k}$) and states just prior to and at time
 191 of recovery ($t_{r,k}$) are known. Finally, we also have animals that are tagged and not recovered
 192 at the time of analysis ($t_{a,k}$) as in conventional tagging experiments. Thus, the data for an
 193 IAT are

$$\{\mathbf{Y}_{III,k}, \mathbf{t}_{III,k}\} = \begin{cases} \mathbf{Y}_{I,k}, \mathbf{t}_{I,k} & \text{if } Y(t_{e,k}) \in \mathcal{F} \\ \mathbf{Y}_{I,k}, \mathbf{t}_{I,k}, Y(t_{e,k}), Y(t_{r,k-}), Y(t_{r,k}), t_{r,k} & \text{if } Y(t_{e,k}) \in \mathcal{R} \text{ and } Y(t_{a,k}) \in \mathcal{F} \\ \{Y(t_{a,k}) \in \{\mathcal{R}, \mathcal{M}\}\} & \text{otherwise} \end{cases} .$$

The probability function for the set of observations from an IAT is

$$\begin{aligned} \mathcal{P}_{III,k}(\mathbf{Y}_{III,k}, \mathbf{t}_{III,k} | t_{0,k}, t_{a,k}, Y(t_{0,k})) &= \mathcal{P}_{I,k}(\mathbf{Y}_{I,k}, \mathbf{t}_{I,k} | t_{0,k}, Y(t_{0,k}))^{I(Y(t_{a,k}) \in \mathcal{F})} \\ &\times \left\{ P_{Y(t_{e,k}), Y(t_{r,k-})} a_{Y(t_{r,k-}), Y(t_{r,k})} \right\}^{I(Y(t_{e,k}) \in \mathcal{R}, Y(t_{a,k}) \in \mathcal{F})} \\ &\times \left\{ \sum_{Y(t_{a,k}) \in \{\mathcal{R}, \mathcal{M}\}}^H P_{Y(t_{0,k}), Y(t_{a,k})} \right\}^{I(Y(t_{a,k}) \in \{\mathcal{R}, \mathcal{M}\})} \end{aligned} \quad (6)$$

194 where $\mathcal{P}_{I,k}(\mathbf{Y}_{I,k}, \mathbf{t}_{I,k} | t_{0,k}, Y(t_{0,k}))$ is the component representing continuous-time observation
 195 between times $t_{0,k}$ and $t_{e,k}$ (i.e., eq. 3), the second line represents the observation of recovery
 196 after battery expiration (analogous to the first line in eq. 5) and the final line represents the
 197 observation of an animal that remains unrecovered at the time of analysis (analogous to the
 198 second line in eq. 5). As with the release time for PSATs, we assume that the battery life
 199 ($t_{e,k}$) of an IAT is fixed or at least independent of the process $Y(\cdot)$ in eq. 6.

200 3. Behavior of MLEs for conventional and archival tagging experiments

201 Through simulation, we explored the behavior of MLEs for the regional migration and
 202 mortality rate parameters based on the three likelihoods presented above for conventional,
 203 PSAT and IAT observations. We intend the process observed through the tagging experi-

204 ments to reflect the life history of adult western Atlantic bluefin tuna. The northern Atlantic
 205 Ocean is split into western and eastern regions at the 45°W meridian for international har-
 206 vest management (e.g., ICCAT, 2007) and fish may migrate between western and eastern
 207 regions of the Atlantic Ocean and die from harvest or natural causes in either region.

208 We assumed instantaneous west-to-east ($\mu_{W,E}$) and east-to-west ($\mu_{E,W}$) migration rates,
 209 region-specific instantaneous harvest (F_W and F_E) and natural mortality (M_W and M_E)
 210 rates are constant throughout the time of analysis for each animal to reduce the complexity
 211 of the results and better observe the behavior of the MLEs for the six instantaneous rate
 212 parameters. Thus, the instantaneous transition matrix we use throughout simulations is

$$\mathbf{A} = \begin{pmatrix} a_{1,1} & \mu_{W,E} & F_W & 0 & M_W & 0 \\ \mu_{E,W} & a_{2,2} & 0 & F_E & 0 & M_E \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \end{pmatrix} \quad (7)$$

213 where $a_{1,1} = -(\mu_{W,E} + F_W + M_W)$, $a_{2,2} = -(\mu_{E,W} + F_E + M_E)$ and $\mathbf{0}$ is a 4×1 column vector.
 214 Notice that states 1 and 2 (alive in the western and eastern Atlantic Ocean) comprise the
 215 subset \mathcal{R} , states 3 and 4 (harvested in the western and eastern Atlantic Ocean) comprise \mathcal{F}
 216 and states 5 and 6 (natural mortality in the western and eastern Atlantic Ocean) comprise
 217 \mathcal{M} . The values we assumed for harvest and natural mortality ($F_W = 0.18$, $F_E = 0.35$,
 218 $M_W = 0.1$ and $M_E = 0.15$) are similar to those stock assessment scientists believe to operate
 219 on adult Atlantic bluefin tuna in the western and eastern Atlantic Ocean based on population
 220 dynamics models (ICCAT, 2007). The western-to-eastern and eastern-to-western Atlantic
 221 migration rates we assumed ($\mu_{W,E} = 0.073$ and $\mu_{E,W} = 0.066$, respectively) were estimated
 222 from probabilities of western Atlantic bluefin tuna being in different regions of the Atlantic at
 223 times subsequent to PSAT experiments reported by Block, Teo, Walli, Boustany, Stokesbury,
 224 Farwell, Weng, Dewar and Williams (2005). All rates are on the scale of yearly time units.

225 The general algorithm for simulating the transition history is the same for all tag types.
 226 The animal is released in a given region ($Y(t_{0,k}) \in \mathcal{R}$) and the waiting time until the animal

227 either leaves the region or dies in the region is an exponential random variable with rate
 228 parameter $-a_{h,h}$. Given that the animal either leaves or dies, the $(H-1) \times 1$ indicator vector
 229 for the next state is a multinomial random variable with probabilities, $-a_{h,i}/a_{h,h}, i \neq h$ (e.g.,
 230 Taylor and Karlin, 1984, pp. 253-255). This procedure is repeated until the analysis time
 231 is reached or the animal dies. As described above, each tag type yields observations with
 232 different information on the process. We simulated 1000 experiments for each experiment
 233 type. Experiment type is defined by the type of tag used (PSAT, IAT or conventional tag),
 234 the total number of tags released and the proportion released in each of the 2 regions. We
 235 generated data and calculated likelihoods for each experiment using C programs compiled
 236 for R (R Development Core Team, 2006).

237 For each simulated experiment we calculated MLEs and, when non-trivial (i.e, non-
 238 infinite) variance estimation was possible, estimated coefficients of variation (CVs) and ap-
 239 proximate 95% confidence intervals for each of the six instantaneous rate parameters so that
 240 we could compare bias, precision and 95% confidence interval coverage, $\psi(0.95)$, of different
 241 experiment types. As the possibility of making inferences is as important as (or more im-
 242 portant than) the behavior of inference procedures when it is possible to use them, we also
 243 calculated the proportion of experiments where non-trivial variance estimates were possible
 244 (ϕ) for each experiment type.

245 We maximized the likelihoods in the log-space of the instantaneous rate parameters to
 246 avoid boundary problems using the Nelder-Mead algorithm of the `optim` function in R (R
 247 Development Core Team, 2006) and variance estimates were based on numerically-derived
 248 hessian matrices in the corresponding space. We calculated asymmetric confidence inter-
 249 vals as $\exp \left\{ \log(\widehat{a}_{i,j}) \pm z_{0.975} \widehat{CV}(\widehat{a}_{i,j}) \right\}$ where $\widehat{CV}(\widehat{a}_{i,j}) = \widehat{SE} \left\{ \log(\widehat{a}_{i,j}) \right\}$ by Taylor series
 250 approximation.

251 There is a high incidence of release of the tag prior to the scheduled time from causes
 252 other than mortality (e.g., Sibert et al., 2006) which we assume is independent of the FSCT
 253 process. In our simulation of PSAT experiments, we modeled the release time of the tag

254 $(t_{a,k})$ using a Bernoulli-beta distribution: indication of tag release prior to the scheduled time
 255 is a Bernoulli random variable with probability p and given the tag releases early, the time
 256 of release scaled by the scheduled release time is a beta random variable with parameters, a
 257 and b . We used values for Bernoulli-beta parameters that we estimated from release times
 258 of pop-up tags that have been deployed by M. E. Lutcavage and colleagues (Figure 1). We
 259 assumed that the scheduled time of release for tags is 0.83 years (10 months) which is similar
 260 to the intended release time of current PSATs. For IATs and conventional tags, we assumed
 261 the time of analysis is 5 years after the time of release and the battery life of IATs is similar
 262 to that of batteries currently used (2 years).

263 3.1 *Simulation Results*

264 When tag releases are allocated equally to both regions the probability of non-trivial
 265 variance estimation for MLEs of the assumed instantaneous rates converges to one for all
 266 tag types, as the total number of released tags increases (Figure 2, row 1). However, the rate
 267 of convergence of the probability of non-trivial variance estimation is generally higher for
 268 harvest rate MLEs than migration and natural mortality rate MLEs. The rate of convergence
 269 is lowest for PSATs which is at least partially due to the shorter length of observation allowed
 270 per tag (≤ 0.83 years). The rate of convergence is similar for experiments using IATs and
 271 conventional tags.

272 Given non-trivial variance estimation is possible, bias of the MLEs diminishes with total
 273 number of released tags for all tag types, but the rate of convergence to unbiasedness is
 274 highest for harvest rate MLEs (Figure 2, row 2). The rate of convergence to unbiasedness
 275 of MLEs is lowest for PSATs except that convergence rate of the MLE for the natural
 276 mortality rate in the western region of the Atlantic Ocean (M_W) is lowest for conventional
 277 tagging experiments.

278 The precision of MLEs for all migration and mortality parameters increases with total
 279 number of released tags similarly for all types of tags when non-trivial variance estimation is
 280 possible (Figure 2, row 3). For a given total number of released tags, the CV of estimators

281 for migration and harvest mortality parameters are lower for IATs and conventional tags
 282 than PSATs and the CV of the natural mortality rate in the western region is lowest when
 283 conventional tags are used.

284 The coverage of 95% confidence intervals converges to the appropriate probability for all
 285 types of tagging experiments as total number of released tags increases (Figure 2, row 4).
 286 The rate of convergence is highest for MLEs of harvest rates, but lowest for the MLE of
 287 the natural mortality rate in the western region (M_W) using IATs and conventional tags in
 288 particular.

289 Considering the allocation of 200 tags to each region, there is generally a higher prob-
 290 ability of non-trivial variance estimation for all MLEs using IATs and conventional tags
 291 ($\phi > 0.8$) than using PSATs when not all tags are released in a single region (Figure 3,
 292 row 1). For PSAT experiments, ϕ increases for rates of transition from alive in the western
 293 region to other states ($\mu_{W,E}$, F_W and M_W) or from alive in the eastern region to other states
 294 ($\mu_{E,W}$, F_E and M_E) as the proportion of tags released in the respective regions increases.
 295 For experiments using IATs, the same relationship occurs for harvested mortality rates, but
 296 ϕ for migration rates and natural mortality rates is highest ($\phi > 0.9$) when all tags are not
 297 released in a single region. The probability of non-trivial variance estimation also increases
 298 for MLEs of the rates of migration from western to eastern regions and western natural
 299 mortality as the proportion of tags released in western region increases using conventional
 300 tags, but this relationship does not hold for the eastern region.

301 Given that non-trivial variance estimation is possible for an experiment, the relative bias
 302 is least in absolute percentage ($|\% \text{Relative Bias}| \sim 0 - 10\%$) for all MLEs when all tags
 303 are not released in a single region (Figure 3, row 2). When all tags are released in a single
 304 region relative bias of some MLEs can be greater than 100% using PSATs or conventional
 305 tags and greater than 50% using IAT tags. For experiments using PSATs, relative bias
 306 for MLEs of mortality or emigration rates increase as the proportion of tags released in the
 307 corresponding region decreases. The relative bias of MLEs of F_W , M_W and $\mu_{W,E}$ also increase

308 as the proportion of conventional tags released in the western region decreases. Relative bias
 309 of M_W and M_E using IATs is positive when no tags are released in the respective regions
 310 and negative when all tags are released in the respective regions.

311 For all tag types, coefficients of variation (CVs) are generally greatest when all tags
 312 are released in a single region (Figure 3, row 3). The CVs generally decrease for rates of
 313 transition from alive in the western region to other states ($\mu_{W,E}$, F_W and M_W) or from alive
 314 in the eastern region to other states ($\mu_{E,W}$, F_E and M_E) as the proportion of tags released
 315 in the respective regions increase. When tags are not released in a single region, CVs of all
 316 MLEs are similar for all tag types and a given allocation.

317 The probability of 95% confidence interval coverage is generally negligibly biased for all
 318 types of tagging experiments when not all tags are release in one region (Figure 3, row 4).
 319 However, confidence interval coverage can be poor for archival tag experiments when all tags
 320 are released in a single region ($\psi(0.95) < 0.80$). Using PSATs, confidence interval coverage
 321 converges to unbiasedness for rates of transition from alive in the western region to other
 322 states ($\mu_{W,E}$, F_W and M_W) or from alive in the eastern region to other states ($\mu_{E,W}$, F_E
 323 and M_E) as the proportion of tags released in the respective regions increase. Using IATs,
 324 confidence intervals are too conservative for natural mortality rates when all tags are released
 325 in a single region and for the rate of migration out of the western region when all tags are
 326 released in the eastern region and vice versa ($\psi(0.95) > 0.99$). When all tags are released in
 327 eastern region, confidence interval coverage for the MLE of F_W is strongly negatively biased
 328 using any type of tag, but the same bias in the MLE of F_E only occurs using PSATs when
 329 all tags are released in the western region.

330 4. An example: Atlantic bluefin tuna conventional tagging data

331 Conventional tagging experiments for Atlantic bluefin tuna have been conducted through-
 332 out the northern Atlantic Ocean for several decades and the resulting data have been archived
 333 by the International Commission for the Conservation of Atlantic Tunas (ICCAT). We con-
 334 sidered a subset of the archived data where tagged fish were released in 1990-1994 and

335 recaptures were made prior to the beginning of 1995 (assumed end of study). We used
 336 the longitudes of tagged fish at release and recovery to determine the regional locations at
 337 those times. The dates of release and recovery are used to determine the times on study
 338 ($t_{a,k} - t_{0,k} \leq 5$ years). Of the 2022 tagged fish released in the western region of the Atlantic
 339 Ocean, 65 were recaptured in the same region and 6 were recaptured in the eastern region.
 340 Of the 4288 tagged fish released in the eastern region, 72 were recaptured in the same region
 341 and 6 were recaptured in the western region (Figure 4).

342 For this example, we have the same instantaneous rates as the simulation study above,
 343 but the probability of reporting harvested tags is thought to be substantially less than
 344 1. Because there is no auxiliary information to estimate reporting probability and it is
 345 completely confounded with natural mortality rates, we assume a value for natural mortality
 346 rate ($M_W = M_E = 0.15$) similar to values believed by Atlantic bluefin assessment scientists
 347 (ICCAT, 2007) and estimate reporting probability ($0 \leq \rho \leq 1$) along with migration and
 348 fishing mortality rates. The resulting instantaneous transition matrix is

$$\mathbf{A} = \begin{pmatrix} a_{1,1} & \mu_{W,E} & \rho_W F_W & 0 & (1 - \rho_W)F_W + M_W & 0 \\ \mu_{E,W} & a_{2,2} & 0 & \rho_E F_E & 0 & (1 - \rho_E)F_E + M_E \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \end{pmatrix} \quad (8)$$

349 where $a_{1,1} = -(\mu_{W,E} + F_W + M_W)$, $a_{2,2} = -(\mu_{E,W} + F_E + M_E)$ and $\mathbf{0}$ is a 4×1 column vector.
 350 We fit a suite of nested models where all rates are the same for each region ($\mu_{W,E} = \mu_{E,W}$,
 351 $F_W = F_E$ and $\rho_W = \rho_E$; m_0), only harvest mortality rates are region-specific (m_1), harvest
 352 and migration rates are region-specific (m_2), migration rates are region-specific and harvest
 353 rates are both region- and year-specific (m_3) and reporting probability is also region-specific
 354 (m_4).

355 For each model, we maximized eq. 5 with respect to the migration and mortality rates
 356 where the necessary probabilities are calculated using eq. 1 (year-specific for models m_3
 357 and m_4). For the best model, we estimated variances and calculated asymmetric confidence

358 intervals for the migration and mortality rates using the same methods as the simulation
359 study above, but a logit transformation of reporting probability is estimated due to its
360 constraints.

361 Through likelihood ratio testing, the model with region- and year-specific harvest mortal-
362 ity rates and region-specific migration rates (m_3) provides the best fit to the Atlantic bluefin
363 tuna data (Table 1). Based on model m_3 , there is evidence of a very low tag reporting prob-
364 ability from harvested individuals (~ 0.122) and estimates of harvest mortality are greater
365 for the western region than the eastern region within a given year, but the estimates tend to
366 decrease over time for a given region (Table 2). The migration rate from the western region
367 to eastern region of the Atlantic Ocean is greater than the opposite migration rate which
368 would result in a in a greater probability of living individuals occurring in the eastern region
369 over time.

370 5. Discussion

371 The results we present here demonstrate that the finite-state continuous-time approach
372 is useful for combining information from the different tagging studies to estimate migration
373 and mortality rates. Current population dynamics models used for fisheries management
374 usually focus on regional populations and parameterize mortality rates instantaneously and,
375 for migratory species, some models make the practical but undesirable assumption that
376 migration and mortality happening in separate intervals (e.g., Hampton and Fournier, 2001).
377 More general models that consider instantaneous migration that “competes” with mortality
378 sources simultaneously using a finite-state continuous-time framework could make use of the
379 likelihoods we propose when conventional and(or) archival tagging data are available.

380 Although we partition space and parameterize the FSCT process for fisheries manage-
381 ment, the partitioning and parametrization can also address behavioral or ecological char-
382 acteristics of the population of interest. With Atlantic bluefin tuna for example, we might
383 further partition the space to represent spawning and feeding grounds within each region
384 because adults are thought to migrate between these areas during certain periods each year.

385 We might also constrain migration rates to the spawning and feeding grounds to be higher
 386 at the appropriate periods to reflect these life history attributes of the population. The
 387 regional migration and mortality model is also directly applicable to management regimes
 388 for many species that employ protected areas where no harvest is allowed (e.g., Roberts,
 389 Bohnsack, Gell, Hawkins and Goodridge, 2001; Field, Punt, Methot and Thompson, 2006).
 390 Harvest rates would be set equal to zero in the protected areas and migration rates among
 391 the protected and unprotected areas could be estimated from tagged animals.

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 398

399 REFERENCES

- 400 Albert, A. (1962). Estimating the infinitesimal generator of a continuous time, finite state
 401 Markov process. *Annals of Mathematical Statistics* **33**, 727–753.
- 402 Andersen, P. K., Borgen, Ø., Gill, R. D. and Keiding, N. (1993). *Statistical models based on*
 403 *counting processes*. Springer-Verlag, New York.
- 404 Andersen, P. K. and Keiding, N. (2002). Multi-state models for event history analysis.
 405 *Statistical Methods in Medical Research* **11**, 91–115.
- 406 Block, B. A., Dewar, H., Blackwell, S. B., Williams, T. D., Prince, E. D., Farwell, C. J.,
 407 Boustany, A., Teo, S. L. H., Seitz, A. and Walli, A. (2001). Migratory movements, depth
 408 preference, and thermal biology of Atlantic bluefin tuna. *Science* **293**, 1310–1314.
- 409 Block, B. A., Teo, S. L. H., Walli, A., Boustany, A., Stokesbury, M. J. W., Farwell, C. J.,

- 410 Weng, K. C., Dewar, H. and Williams, T. D. (2005). Electronic tagging and population
411 structure of Atlantic bluefin tuna. *Nature* **434**, 1121–1127.
- 412 Bonfil, R., Meÿer, M., Scholl, M. C., Johnson, R., O’Brien, S., Oosthuizen, H., Swanson,
413 S., Kotze, D. and Paterson, M. (2005). Transoceanic migration, spatial dynamics and
414 population linkages of white sharks. *Science* **310**, 100–103.
- 415 Chapman, D. G. (1961). Statistical problems in the dynamics of exploited fisheries popula-
416 tions. *Proceedings of the Berkeley Symposium on Mathematical Statistics and Probability*
417 **4**, 153–168.
- 418 Commenges, D. (2002). Inference for multi-state models from interval-censored data. *Sta-*
419 *tistical Methods in Medical Research* **11**, 167–182.
- 420 Cox, D. R. and Miller, H. D. (1965). *The Theory of Stochastic Processes*. John Wiley &
421 Sons, New York.
- 422 Darroch, J. N. (1958). Estimation of a closed population. *Biometrika* **45**, 343–359.
- 423 Dupont, W. D. (1983). A stochastic catch-effort method for estimating animal abundance.
424 *Biometrics* **39**, 1021–1033.
- 425 Field, J. C., Punt, A. E., Methot, R. D. and Thompson, C. J. (2006). Does MPA mean ‘Major
426 Problem for Assessments’? considering the consequences of place-based management
427 systems. *Fish and Fisheries* **7**, 284–302.
- 428 Hampton, J. and Fournier, D. A. (2001). A spatially, disaggregated, length-based, age-
429 structured population model of yellowfin tuna (*Thunnus albacares*) in the western and
430 central Pacific Ocean. *Marine and Freshwater Research* **52**, 937–963.
- 431 Hearn, W. S., Sundland, R. L. and Hampton, J. (1987). Robust estimation of the natural
432 mortality rate in a completed tagging experiment with variable fishing intensity. *Journal*
433 *Du Conseil International Pour L’exploration De La Mer* **43**, 107–117.
- 434 Hestbeck, J. B., Nichols, J. D. and Malecki, R. A. (1991). Estimates of movement and site
435 fidelity using mark-resight data of wintering Canada geese. *Ecology* **72**, 523–533.
- 436 Hilborn, R. (1990). Determination of fish movement patterns from tag-recoveries using

- 437 maximum likelihood estimators. *Canadian Journal of Fisheries and Aquatic Sciences*
438 **47**, 635–643.
- 439 Hoem, J. M. (1971). Point estimation of forces of transition in demographic models. *Journal*
440 *of the Royal Statistical Society. Series B* **33**, 275–289.
- 441 ICCAT (2007). Report of the 2006 Atlantic bluefin tuna stock assessment session. *Collective*
442 *Volume of Scientific Papers ICCAT* **60**.
- 443 Kalbfleisch, J. D. and Lawless, J. F. (1985). The analysis of panel data under a Markov
444 assumption. *Journal of the American Statistical Association* **80**, 863–871.
- 445 Kalbfleisch, J. D. and Prentice, R. L. (2002). *The statistical analysis of failure time data*.
446 Wiley & Sons, New York.
- 447 Karlin, S. and Taylor, H. M. (1975). *A first course in stochastic processes*. Academic Press,
448 New York.
- 449 Laslett, G. M., Eveson, J. P. and Polacheck, T. (2002). A flexible maximum likelihood
450 approach for fitting growth curves to tag-recapture data. *Canadian Journal of Fisheries*
451 *and Aquatic Sciences* **59**, 976–986.
- 452 Lebreton, J. D. and Pradel, R. (2002). Multistate recapture models: modelling incomplete
453 individual histories. *Journal of Applied Statistics* **29**, 353–369.
- 454 Nichols, J. D. and Kendall, W. L. (1995). The use of multi-state capture-recapture models
455 to address questions in evolutionary ecology. *Journal of Applied Statistics* **22**, 835–846.
- 456 Pollock, K. H. (1991). Modeling capture, recapture, and removal statistics for estimation
457 of demographic parameters for fish and wildlife populations: past, present, and future.
458 *Journal of the American Statistical Association* **86**, 225–238.
- 459 Quinn, T. J. and Deriso, R. B. (1999). *Quantitative Fish Dynamics*. Oxford University
460 Press. 542pp.
- 461 R Development Core Team (2006). *R: A Language and Environment for Statistical Com-*
462 *puting*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0.
- 463 Ricker, W. E. (1975). *Computation and the interpretation of biological statistics of fish*

- 464 *populations*. Bulletin of the Fisheries Research Board of Canada, Number 191. 382pp.
- 465 Roberts, C. M., Bohnsack, J. A., Gell, F., Hawkins, J. P. and Goodridge, R. (2001). Effects
466 of marine reserves on adjacent fisheries. *Science* **294**, 1920–1923.
- 467 Schwarz, C. J., Schweigert, J. F. and Arnason, A. N. (1993). Estimating migration rates
468 using tag-recovery data. *Biometrics* **49**, 177–193.
- 469 Schwarz, C. J. and Seber, G. A. F. (1999). Estimating animal abundance: review III.
470 *Statistical Science* **14**, 427–456.
- 471 Seber, G. A. F. (1982). *The Estimation of Animal Abundance and Related Parameters*. C.
472 Griffin & Co., Ltd., London. 654pp.
- 473 Seber, G. A. F. and Schwarz, C. J. (2002). Capture-recapture: before and after EURING
474 2000. *Journal of Applied Statistics* **29**, 5–18.
- 475 Sibert, J. R., Lutcavage, M. E., Nielsen, A., Brill, R. W. and Wilson, S. G. (2006). Interan-
476 nual variation in large scale movement of Atlantic bluefin tuna (*Thunnus, thynnus*) de-
477 termined from pop-up satellite archival tags. *Canadian Journal of Fisheries and Aquatic*
478 *Sciences* **63**, 2154–2166.
- 479 Sibert, J. R., Musyl, M. K. and Brill, R. W. (2003). Horizontal movement of bigeye tuna
480 (*Thunnus obesus*) near Hawaii determined by Kalman filter analysis of archival tagging
481 data. *Fisheries Oceanography* **12**, 141–151.
- 482 Taylor, H. M. and Karlin, S. (1984). *An Introduction to Stochastic Modeling*. Academic
483 Press, Orlando, Florida USA.
- 484 Taylor, N. G., Walters, C. J. and Martell, S. J. D. (2005). A new likelihood for simultaneously
485 estimating von bertalanffy growth parameters, gear selectivity and natural and fishing
486 mortality. *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 215–223.
- 487 Whitehead, H. (2001). Analysis of animal movement using opportunistic individual identi-
488 fications: application to sperm whales. *Ecology* **82**, 1417–1432.

Table 1

Sequential likelihood ratio tests of nested models fit to Atlantic bluefin tuna tagging data. The number of parameters (n_p) and p-values (P) are provided.

Model	$\log(L)$	n_p	P
m_0	-1786.65	3	
m_1	-1780.38	4	0.0004
m_2	-1776.26	5	0.0041
m_3	-1752.03	13	8.067×10^{-8}
m_4	-1750.81	14	0.1183

Table 2

Parameter estimates and asymmetric 95% confidence intervals provided by model m_3 from fitting Atlantic bluefin tuna tagging data.

parameter	estimate	SE	CI
$\mu_{W,E}$	0.1832	0.0750	(0.0821 - 0.4089)
$\mu_{E,W}$	0.0374	0.0158	(0.0164 - 0.0855)
$F_{W,1990}$	0.5168	0.2491	(0.2009 - 1.3292)
$F_{E,1990}$	0.1773	0.0816	(0.0719 - 0.4369)
$F_{W,1991}$	0.3946	0.1545	(0.1832 - 0.8498)
$F_{E,1991}$	0.1360	0.0538	(0.0627 - 0.2953)
$F_{W,1992}$	0.1255	0.0580	(0.0507 - 0.3107)
$F_{E,1992}$	0.0370	0.0167	(0.0153 - 0.0895)
$F_{W,1993}$	0.1256	0.0584	(0.0505 - 0.3123)
$F_{E,1993}$	0.0641	0.0279	(0.0273 - 0.1505)
$F_{W,1994}$	0.0910	0.0523	(0.0295 - 0.2809)
$F_{E,1994}$	0.0300	0.0157	(0.0107 - 0.0838)
ρ	0.1222	0.0063	(0.0630 - 0.2238)

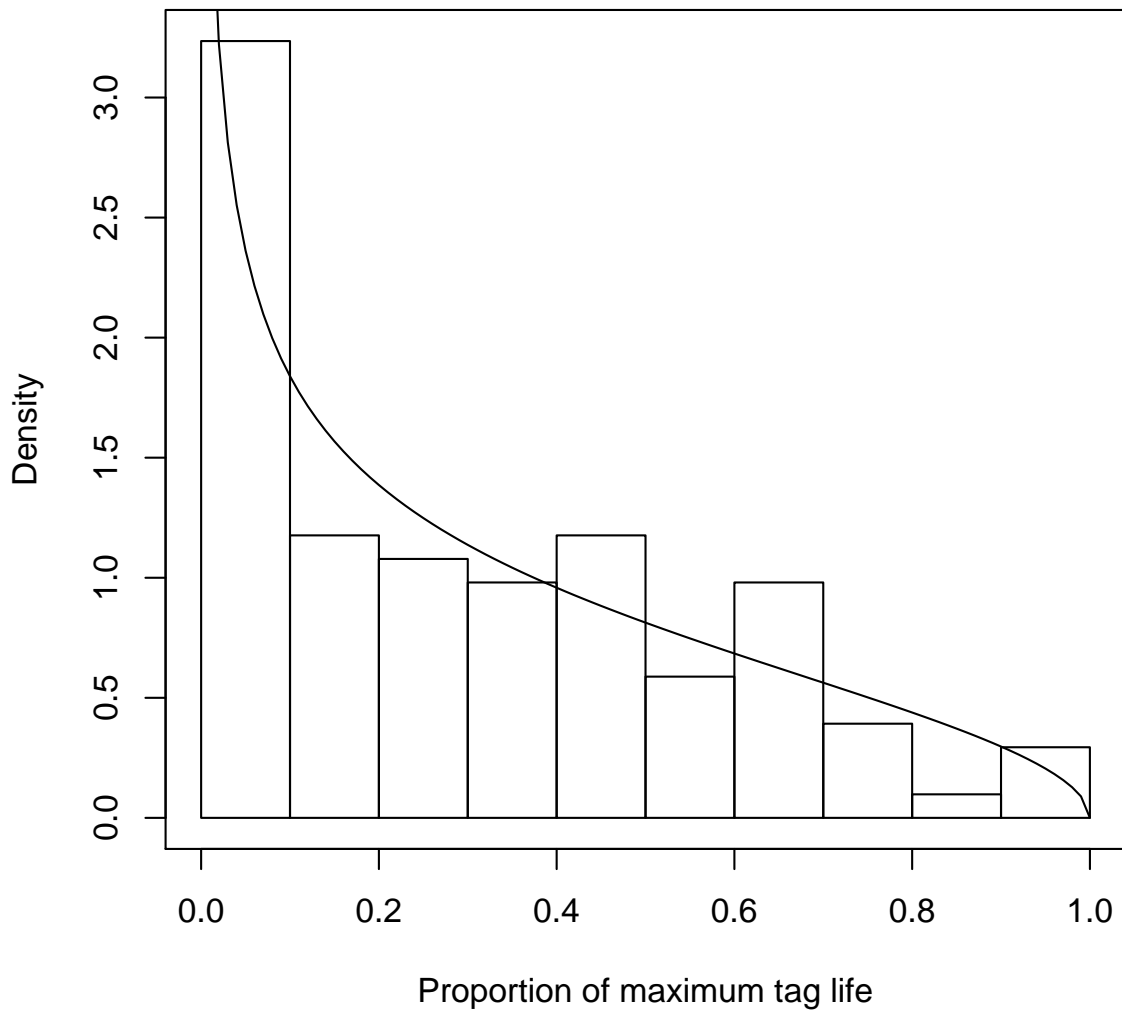


Figure 1. Distribution of the scaled release times of prematurely released pop-up satellite archival tags scheduled to release greater than 250 days after deployment ($n = 192$). The curve represents a beta distribution with parameters ($a = 0.6785472$, $b = 1.508478$) determined by fitting the scaled release times. The probability of premature release is $p = 0.2554745$.

